FLIGHT BEHAVIOR OF THE RED-FOOTED BOOBY

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From 14 February to 9 May 1958, a study of the breeding biology of the Red-footed Booby (*Sula s. sula*) was undertaken at Half Moon Cay, 50 miles east of Belize, British Honduras. The results of that study have been presented in an earlier paper (Verner, 1961); the purpose of the present paper is to report observations on various aspects of flight and flocking behavior in this species.

To become airborne, the boobies normally launch into the wind from an elevated perch; they also take flight from the ground with ease when heading into a wind. When there is no wind, however, they fly from the ground only with difficulty, half running and half flying for several feet before finally achieving full flight. To fly from the surface of the water they jump forward suddenly into the wind by thrusting backward with both feet simultaneously, in the manner of pelicans.

Ordinarily the boobies alternate a few flaps of the wings with short glides but were occasionally seen to glide more than a mile without flapping. They display great agility in gliding long distances above the surface of the sea, just clearing the crest of each wave without stroking their wings, even when there is relatively little perceptible wind on shore. Their flock patterns have been described as lines and wedges (Maynard, 1889), and Gifford (1913) stated that "members of a flock are practically synchronous in every action." My observations of flocks near the breeding colony at Half Moon Cay, on the other hand, indicate that disorder was the rule. Rarely, flocks formed irregular ranks or files that were maintained at most only a few seconds. The composition of flocks was very dynamic, individuals leaving and joining groups and flocks splitting or combining frequently. Perfect synchrony in the flap–glide actions of members of a flock was sporadic at best, and the extent of asynchrony increased with increasing flock size.

FLIGHT TO AND FROM THE CAY

Each day great numbers of boobies left the colony early in the morning, spent the day fishing, and returned to the colony in the evening. Night flying occurred but probably not to an appreciable extent (cf. Sharpe, 1904). The main fishing grounds apparently lay to the east of the cay, since birds *always* departed toward, and returned from, the east. If there was sufficient wind in the morning to create an updraft against the vegetation at the windward side of the island, the boobies congregated in the updraft as a soaring group from which individuals and smaller groups departed for the day's

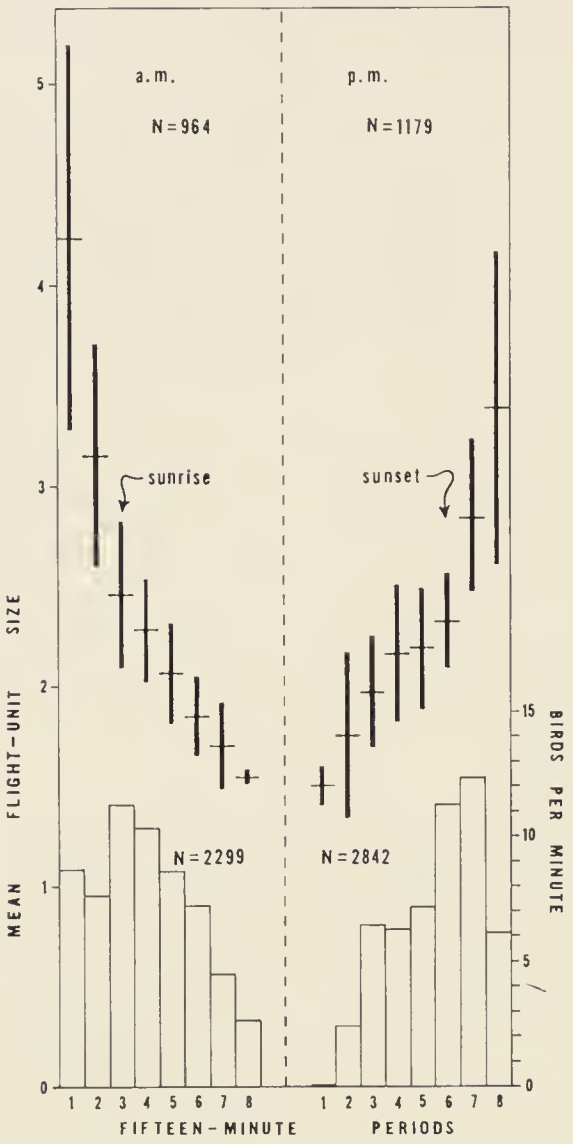

Fig. 1. Mean sizes of flight units (left scale) during each count period are shown above with two standard errors plotted on each side of the mean. Flight density (right scale) is shown in the lower histogram. The number of flight units is indicated above and the number of birds below. Results for AM are based on three days' records, combined on the basis of sunrise time; those for PM are based on four days' counts combined by sunset time.

fishing. The position of this soaring group shifted with changes in wind direction but had no influence on the final easterly orientation of departing birds. The departure began before daylight, reached a peak within 10 minutes of sunrise (the exact time varying with sky and wind conditions), and was nearly completed by an hour after sunrise (Fig. 1).

Although boobies flew to and from the colony all day, movement was negligible from an hour after sunrise to an hour before sunset. In 100 minutes of observing between 1050 and 1200 on 2 days, 44 birds left the colony and two entered it; and from 1400 to 1600 on one afternoon only

17 birds entered the colony and none left. The mean size of flight units during these periods was 1.4 ± 0.14 ($N = 44$) (the term flight unit being used here designates any solitary bird or group of birds). The largest flight unit noted consisted of 36 birds leaving the colony just before daylight on 5 March. Mean flight-unit size in the early morning was 2.4 ± 0.07 ($N = 964$) and that in late evening was 2.4 ± 0.06 ($N = 1{,}179$).

Examination of Figure 1 reveals that the mean flight-unit size decreased steadily during the morning and increased steadily during the evening. The same, however, was not true of the number of birds per minute (flight density) passing the point of observation. Flight-unit size in each succeeding 15-minute count period was independent of that in the preceding count period, since new birds, hence entirely new flight units, were passing continuously.

Applying the Spearman Rank Correlation Coefficient (r_s) to combined results of morning and evening count periods indicates a significant correlation ($r_s = 0.78$, $P < 0.01$) between mean flight-unit size and the number of birds passing per minute after sunrise and before sunset. Before sunrise and after sunset (periods including sunrise and sunset were grouped with this ranking), however, there is no positive correlation ($r_s = -0.60$) between flight-unit size and flight density. At the same time, there is a strong correlation ($r_s = 1.00$) between increasing flight-unit size and decreasing light intensity, indicating that darkness increases the birds' tendencies to aggregate regardless of their density. This phenomenon suggests that, after dark, groups of birds may navigate more effectively than individuals, making it more advantageous to form groups after dark.

FRIGATEBIRDS AND FLYING BOOBIES

About 20 pairs of Magnificent Frigatebirds (*Fregata magnificens*) nested within the booby colony. The piratic habits of this species are well known, and I observed numerous aerial attacks of the frigatebirds on boobies returning to the colony from a fishing foray. Boobies under attack screeched loudly in a raucous voice and attempted to outmaneuver the larger birds—often diving at great speeds in amongst the treetops. Frequently the frigatebirds seized a wing tip or the tail of the booby in attempts to make it disgorge its catch (cf. Lawry, 1926). Food regurgitated by the booby was either caught in midair by the frigatebird or was picked up from the surface of the water. None that landed on the ground was retrieved.

In 86 recorded observations of such attacks, no male frigatebird was involved. If males were equally as likely to attack boobies for food as are females, the probability of obtaining the above result is $(\frac{1}{2})^{86}$, or about one

chance in 7.74×10^{25}. I have been unable to locate any other reference to this division of labor between the sexes and I do not know its significance. Very likely, however, it is related to some other aspect of the species' breeding biology—perhaps a division of labor at the nest. An especially important question in this connection is whether the same situation prevails at times of the year other than the breeding season.

Male frigatebirds *were* seen attempting to secure nest materials from flying boobies, and on one occasion a number of boobies combined to force a flying male frigatebird to abandon some nest materials.

SOARING BEHAVIOR

On evenings when there was sufficient wind to create an updraft at the windward edge of the island, many boobies (likely those just relieved at the nest) formed a soaring group in the updraft. The birds maintained this behavior for long periods, although how long any single individual did so is unknown. If I walked beneath them, they followed above me until I left the area of the updraft. At times, individuals dropped to a lower level to observe me carefully from within 5 or 10 feet (see Farquhar, 1900). Investigative behavior of this sort was most pronounced among subadult birds, many of which were seen observing several feet of the mast of a sailboat, for several minutes at a time, by drifting up and down on outstretched wings within a foot of the structure. Similar behavior was directed toward a lighthouse located near the eastern tip of the island.

Although no clear advantage accrued to birds engaged in this evening soaring behavior, a great deal of time was devoted to it. Possibly, however, this behavior could serve as practice to maintain the fine system of coordination necessary to move rapidly through the air with a minimum of flapping, just as the finest athletes or musicians must practice to maintain the precision of their skills. The boobies' size makes it possible for them to ingest enough food at one time to maintain themselves for several hours without feeding; thus they have time available for other activities. Selection should favor the most efficient utilization of time and energy (Orians, 1961), and if soaring serves as effective practice for gliding it would be adaptive. If this is the selective basis for such behavior, however, the advantage gained from practice must outweigh any disadvantage resulting from the relatively minor energy expenditure involved in soaring. Those birds that glide most efficiently will clearly consume less energy during the many hours each day they are on the wing in search of food.

Surface skimming by the booby has an advantage other than simply permitting low-energy flight, however. Gifford (1913) noted Red-footed

Boobies catching flying fish in the air when they left the water to sail over the surface. I once observed the same behavior by an immature Brown Booby (*Sula leucogaster*) in the Yucatan Channel, between Mexico and Cuba. Such aerobatics require fine control of flight and must involve considerable feedback relative to feather position, wind pressure, and wave action. At least part of this flight system would receive practice during soaring. At Half Moon Cay, flying fish comprised most if not all of the adult diet. although what proportion of this was obtained by the aerial pursuit method cannot be judged.

SUMMARY

Red-footed Boobies rely heavily on wind to take wing, although they can do so without it, even from the ground. In flight they flap and glide alternately and usually fly alone or in small groups with little or no organization. They are capable of gliding long distances just above the wave crests even on relatively calm days.

In flight to and from the feeding grounds the birds left the island early in the morning and returned late in the evening. The mean size of flight units decreased steadily in the morning and increased steadily in the evening, irrespective of the period of greatest flight density. A significant correlation between aggregate size and increasing darkness suggests the possibility that groups navigate with greater accuracy in the dark than individual birds, making it advantageous to form larger groups in the dark.

Boobies under attack from frigatebirds attempted to outmaneuver the larger birds, but were not always successful. In the 86 such attacks noted, only female frigatebirds were involved, although males were seen attacking boobies for nest materials. The significance of this division of labor is unknown, nor is it known if the same situation prevails outside the breeding season.

The boobies devoted much time to soaring when there was no clear advantage to be gained. It is postulated that this activity serves as practice to maintain the precision of flight control necessary for capturing flying fish in flight and for gliding over the crests of waves with a minimum of flapping.

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